

OBSERVATIONS ON *TUBULOVESICULA PINGUIS* (LINTON, 1910)
MANTER, 1947 AND ON SYSTEMATICS OF THE
HEMIUROID TREMATODES¹

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Linton (1940) described *Dinurus pinguis* n. sp. from a large number of marine fishes. The specific description and figures were based on material from *Menidia notata*, with additions from specimens taken from other fishes. *Menidia menidia notata* (Mitchill) was recognized formerly as a northern subspecies, but the subspecies is no longer recognized by leading authorities. Linton admitted that in earlier publications he had assigned these parasites to other, different species, e.g., specimens from *Anguilla rostrata* were identified as *Distomum grandiporum* (1898, page 520), and others from *Roccus lineatus* were referred to *Distomum rufoviride* Rudolphi (1898, page 512). Linton (1901) identified as *Distomum tornatum* Rudolphi specimens from *Fundulus heteroclitus* (page 442), from *Menidia notata* (page 444), and from *Roccus lineatus* (page 455). To *Distomum tornatum* he (1905) assigned specimens from *Synodus foetens* (page 355), *Tylosurus marinus* (page 356) and *Menticirrhus americanus* (page 399), all taken at Beaufort, North Carolina. It is questionable whether or not all of these determinations pertain to the same species. Furthermore, it must be recognized that fishes feed on smaller fishes and parasites of ingested fishes may be found in the digestive tract of predators.

In his (1940) paper, Linton listed the following species as hosts of *Dinurus pinguis*: the American eel, *Anguilla rostrata*; silver hake, *Merluccius bilinearis*; silversides, *Menidia notata*; kingfish, *Menticirrhus saxatilis*; toadfish, *Opsanus tau*; summer flounder, *Paralichthys dentatus*; common gurnard, *Merulinus carolinus*; northern barracuda, *Sphyræna borealis*; and the lizardfish, *Synodus foetens*. The material on which the species *D. pinguis* was based consisted of an assemblage of small trematodes, collected over a period of forty years, and obviously included representatives of more than one species and probably of more than one genus. The specific description was general, indefinite, equivocal and could comprise members of different species or even genera.

Two new genera, *Stomachicola* and *Tubulovesicula*, were erected by Yamaguti (1934) and assigned to the subfamily Dinurinae Looss, 1907. *Stomachicola* was based on *S. muraenesocis* Yamaguti, 1934 from the stomach of *Muraenesox cinereus*, taken in the Inland Sea of Japan and the South China Sea. *Tubulovesicula* was based on *T. spari* Yamaguti, 1934, described on a single specimen from the stomach of *Sparus macrocephalus* taken in the Inland Sea. Included in the genus were two new species; *T. anguillae* from the stomach of *Anguilla japonica* and *T. muraenesocis* from *M. cinereus* taken in the Inland Sea; *T. angusticauda* (Nicoll, 1915) from *M. cinereus* taken in North Queensland and assigned originally to

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Ectenurus Looss, 1907; and *T. lindbergi* (Layman, 1950) from various fishes taken in Peter the Great Bay and assigned originally to the genus *Lecithaster* Lühe, 1901. Manter (1947) discussed the genera of the family Hemiuridae Lühe, 1901 and page 348 compared *Dinurus* Looss, 1907 with other closely related genera: *Ectenurus* Looss, 1907; *Lecithocladium* Lühe, 1901; *Magnacetabulum* Yamaguti, 1934; *Tubulovesicula* Yamaguti, 1934; *Stomachicola* Yamaguti, 1934; and *Erilepturus* Woolcock, 1935. Manter (1947) listed the generic features of *Tubulovesicula* and stated, page 350 "Type species: *T. spari* Yamaguti, 1934. Other species: *T. anguillae* Yamaguti, 1934; *T. muracnesocis* Yamaguti, 1934; *T. californica* Park, 1936; *T. pseudorhombi* Yamaguti, 1938; *T. lindbergi* (Layman, 1930) Yamaguti, 1934; *T. nanaimoensis* (McFarlane, 1935) n. comb. (synonym: *Dinurus nanaimoensis* McFarlane, 1935) *T. pinguis* (Linton, 1940) n. comb. (synonym: *Dinurus pinguis* Linton, 1940); *T. angusticauda* (Nicoll, 1915) Yamaguti, 1934." Manter (1954) discussed the status of species in the genus *Tubulovesicula*. He observed extensive variations in morphology and size of eggs and suppressed *T. californica* Park, 1936; *T. pseudorhombi* Yamaguti, 1938; and *T. muracnesocis* as synonyms of *T. spari*. He gave a key to six recognized species of *Tubulovesicula*. Sogandares-Bernal (1959) redescribed *Tubulovesicula lindbergi* (Layman, 1930) from specimens from the stomach of an unidentified eel and *Synodus* sp. taken near the mouth of Chimán River, Pelado Island, Panama Bay, Panama. He declared that *T. spari* is indistinguishable from *T. lindbergi* and the latter species becomes type of the genus. Sogandares-Bernal recognized only four species, *T. lindbergi* (Layman, 1930); *T. angusticauda* (Nicoll, 1915); *T. magnacetabulum* Yamaguti, 1939; and *T. pinguis* (Linton, 1940). Although various authors have mentioned *Tubulovesicula pinguis*, there is no existing description of the species other than the confused and inadequate accounts of Linton.

MATERIAL AND OBSERVATIONS

During the summer of 1972, examination of a large number of *Menidia menidia* has provided information on the development and adult morphology of *T. pinguis* and permits a redescription of the species. The study was carried on from June 1 to September 15 at the Marine Biological Laboratory in Woods Hole, Massachusetts. The worms were found, not in the stomach but in the body cavity, with the oral suckers attached to the liver or to one of the large intestinal blood vessels. They are blood-suckers and their digestive ceca were filled with blood of the host. This fact accounts for the reddish color of living worms. Occasionally, juvenile specimens were found in the tissues, but always free and never encysted. The incidence of infection varied from ten to forty per cent. The intensity was low, usually one or two worms in a host; the largest number found in a fish was eighteen.

The worms are appendiculate hemiurids, with the ecsoma (retractile tail-like portion of the body) smaller and typically shorter than the trunk or body proper. When the ecsoma is retracted, the posterior end of the body and excretory pore are withdrawn and appear deep within the body. When fully extended, the ecsoma may be as long as the rest of the body and in living worms may measure 3.00 mm in length. In fixed and stained specimens, it is shorter and more retracted.

In general morphology, the worms agree with the generic diagnosis of *Tubulovesicula* as given by Yamaguti (1934, 1958, 1971) but the esophagus bifurcates posteri-

only to form two lateral pouches, all lined with cuticula and provided with powerful muscular walls. In living worms these structures are conspicuous and in constant movement, churning the contents back and forth in all three pockets. These lateral pouches are similar to the "stomachs" or "crops" of other hemiurid trematodes. In the generic diagnosis of *Hirudinella*, Yamaguti (1958, page 252) stated, "esophagus of moderate length; ceca forming "stomach" portion at commencement, often dilated posteriorly with dark ingesta probably due to blood of the host." In the diagnosis of *Tubulovesicula* Yamaguti (1934) did not mention the existence of "stomachs." In his Figure 117, of *T. muraenesocis*, the anterior ends of the ceca are somewhat distended, but the figures of other species included in the genus do not show enlargements. In the diagnosis of *Tubulovesicula*, Yamaguti (1934) reported the specimens from the stomachs of their hosts, but the worms in *M. menidia* are in the body cavity, not in the stomach. Also, Yamaguti did not mention the existence of "stomachs" in the digestive tract. Such lack of agreement, if indeed it exists between the specimens described by Yamaguti and those from *M. menidia*, might suggest generic difference, but since it is not correlated with other disagreements, the species, *pinguis*, is retained in *Tubulovesicula*. To provide a more complete description of the species, figures of developmental stages are presented. Measurements of any specimen depend on the degree of sexual maturity, the particular region and extent of muscular contraction, and the amount of pressure during fixation. The sizes of the suckers and pharynx are less variable than the soft parts and yield the most reliable data.

Specific diagnosis of T. pinguis

Gravid specimens are 3.80 to 6.50 mm long; 0.80 to 1.30 mm wide. The acetabulum, situated in the anterior third of the body, measures 0.38 to 0.48 mm in diameter. In fixed specimens the esoma is about one-fourth as long as the trunk.

Digestive system

The oral sucker is subterminal, 0.18 to 0.25 mm in diameter; the pharynx, adjacent to the oral sucker, is 0.13 to 0.16 mm in diameter. The esophagus is about as long as the pharynx; cervical glands discharge into its anterior portion and posteriorly it communicates with two lateral pouches, termed "stomachs," as reported earlier. The worms are hematophagus and the cervical glands presumably secrete an anticoagulant. The stomachs are slightly larger than the esophagus and measure about 0.16 mm in diameter. On either side, the stomach communicates by a short constricted portion with the cecum of that side. The ceca are lined with tall epithelium and extend the length of the body, terminating blindly near the posterior end.

Male reproductive system

The testes are spherical to oval to triangular, usually longer in the anteroposterior axis, 0.35 to 0.57 mm in diameter, situated immediately or a short distance posterior to the acetabulum. They may be opposite or either one may be slightly in advance. Sperm-ducts arise at their median faces and unite as they enter the posterior end of the seminal vesicle. The vesicle may be tubular, sinuous, or bent at an angle, or

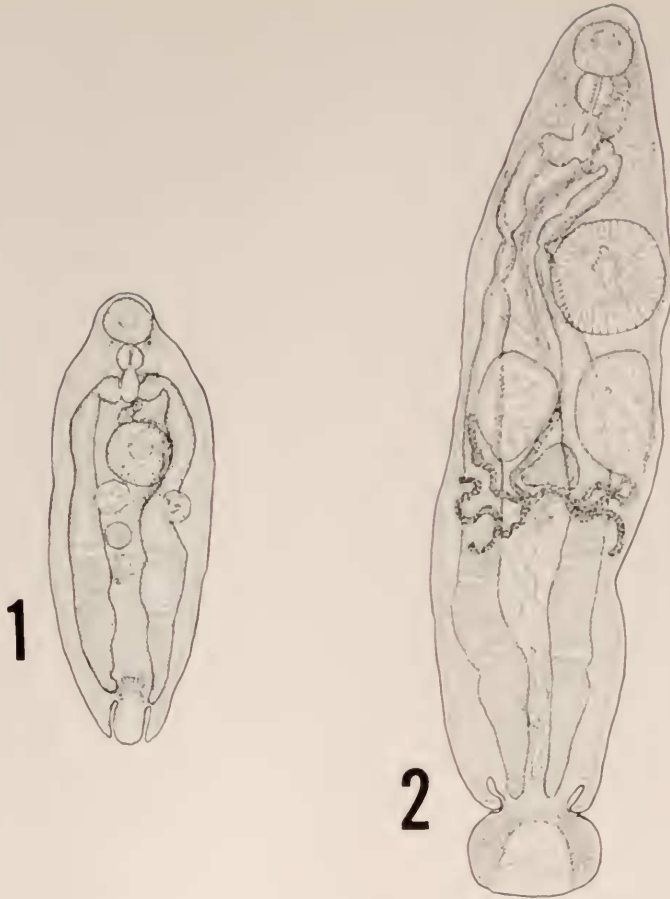


FIGURE 1. A dorsal view of a small, much flattened specimen, 1.00 mm in length. In it the esoma is retracted, the digestive and reproductive systems are clearly portrayed but the reproductive organs are rudimentary. The acetabulum is 0.15, the oral sucker, 0.10, and the pharynx 0.06 mm in diameter.

FIGURE 2. Ventral view of a specimen, 2.00 mm in length. In it the male system is just maturing. There are spermatozoa in the seminal vesicle but the female system is not yet functional. There are no ova and the cells in the vitelline tubules are small, without vitelline droplets in the cytoplasm. The acetabulum is 0.22, the oral sucker is 0.14, and the pharynx is 0.09 mm in diameter.

if filled with spermatozoa it may be saccate, 0.52 by 0.14 mm. The vesicle is anterodorsal to the testes; it is followed by a short, narrow duct that, posterior to the acetabulum, opens into a long, almost straight tube, encased in prostatic cells from its origin to about three-fourths of the distance from the acetabulum to the bifurcation of the digestive tract. Here it loses its covering of glandular cells, coils about for a short distance and joins the metratermal end of the uterus. The hermaphroditic duct enters a tubular to oval muscular sac that opens into the genital atrium. The positions and relations of the genital ducts vary with contractions of

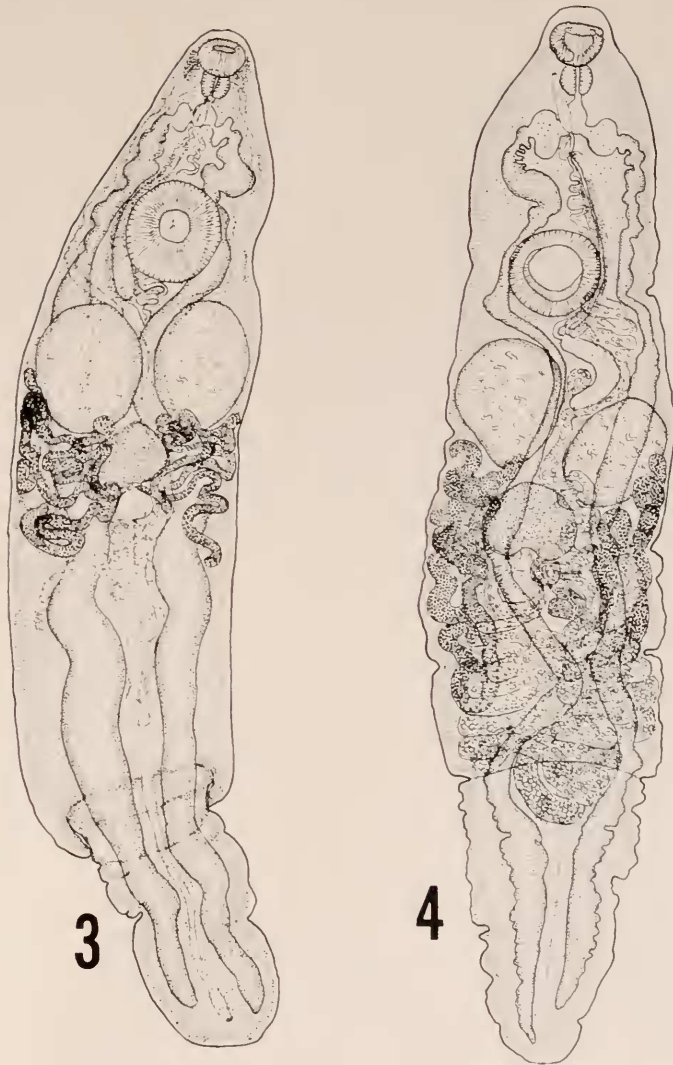


FIGURE 3. Ventral view of a specimen 4.00 mm long. The ecsoma is 0.94 mm long. The worm is fully mature, with eggs in the initial portion of the uterus. In it, the uterine coils are not congested with eggs and other structures are visible. The acetabulum is 0.31, the oral sucker, 0.16, and the pharynx is 0.11 mm in diameter.

FIGURE 4. Dorsal view of a gravid specimen in which the anterior end is well extended and the reproductive ducts are conspicuous. In it the trunk is 3.30 mm long, 1.00 mm wide; the distance between the suckers is 0.65 mm. The ecsoma is 1.30 mm long, the acetabulum is 0.44, the oral sucker, 0.22, and the pharynx is 0.14 mm in diameter. The stomachs are 0.15 mm in diameter. The left testis is 0.50 by 0.47 mm; the right 0.50 by 0.38 mm; the ovary is 0.30 by 0.34 mm; the seminal vesicle is 0.50 by 0.14 mm; and the hermaphroditic muscular sac is 0.10 by 0.04 mm.

the body musculature and are seen best when the anterior region is extended. The genital atrium is narrow and is situated ventral to the pharynx.

Female reproductive system

The ovary is median to submedian, spherical to oval to reniform, often longer in the transverse axis, and 0.30 to 0.50 mm in diameter. The oviduct arises from the posterior face, receives a duct from the seminal receptacle, another from the vitelline reservoir, and enters Mehlis' gland, where it becomes the ootype, and from which the uterus takes origin. The seminal receptacle, which varies in size with the amount of sperm, is located posterior to the ovary, and the initial portion of the uterus may be filled with spermatozoa. The vitellaria consist of long tubular lobes, three on one side and four on the other, which discharge into the common reservoir. A short duct from the reservoir joins the oviduct immediately after the duct from the seminal receptacle. The arrangement of the vitelline lobes is not constant; the set of three may be on either side of the body. The uterus passes posteriad in close coils, often into the ecsoma, and then forward, between the testes, above or beside the acetabulum, and in the preacetabular area it is ventral to the male duct until their junction. Young eggs are thin-shelled, 0.020 by 0.013 mm in average measurement; eggs in the terminal portion of the uterus are thick-shelled, operculate, embryonated, and measure 0.018 by 0.012 mm. Eggs are slightly smaller in fixed and stained specimens.

Excretory system

The pore is almost terminal and the vesicle consists of a median stem which extends forward to the testicular level where it bifurcates and the arms pass anterior and laterad in front of the testes and ventral to the digestive ceca. They continue a forward course to the level of the junction of the oral sucker and pharynx where they turn dorsad and mediad. At this point, each gives off a recurrent tubule and then they join above the posterior end of the oral sucker. This vesicular portion of the excretory system is filled with exceedingly fine globules. The fluid in the recurrent tubules is clear. These tubules pass posteriad, lateral or ventral to the digestive ceca, and receive branches formed by the union of capillaries that drain the flame-cells dispersed throughout the tissues. The body is thick, the parenchyma is dense, the pattern is complex, and details of the system have not been worked out. The only report of the flame-cell pattern in a mature hemiurid was made by Looss (1894) who found 2 [(11 × 32)] or 704 cells in *Azygia lucii*. The same pattern and cell number was found in the body of the cercaria of *Azygia sebago* by Stunkard (1956). Wootton (1957) found the same pattern and number of flame-cells in the body of *Azygia acuminata* and 2 [(5 × 32)] or 320 flame-cells in the tail of that species.

These trematodes from *M. menidia* are strikingly similar to members of the genus *Hirudinella* Garcin, 1730, studied by Nigrelli and Stunkard (1947). They agree in the sanguivorous habit, and the details of the digestive, excretory and reproductive systems. This morphological similarity implies close phylogenetic and systematic affinity. Yamaguti (1971) included Dinurinae Looss, 1906 as a subfamily in the Hemiuridae Lühe, 1901. Baer and Joyeux (1961) recognized Dinuridae Skrjabin and Gushanskaya, 1954 and Hirudinellidae Dollfus, 1932 as families in the superfamily Hemiuroidea.

DISCUSSION

Tubulovesicula and Stomachicola

In a paper entitled, "The *Stomachicola rubea*: *Tubulovesicula pinguis* enigma," Sinclair, Smith and Sullivan (1972) reported *S. rubea* from twenty-eight species of marine fishes collected near Sapelo Island, Georgia, between 1 October, 1969 and the autumn of 1971. The species had been described by Linton (1910) as *Dinurus rubeus* n. sp. Manter (1931) had described *Dinurus magnus* as a new species from *Synodus foetens* taken at Beaufort, North Carolina and noted that it differed from *D. rubeus* in extent of the pars prostatica and seminal vesicle. Both species were transferred by Manter (1947) to the genus *Stomachicola* Yamaguti, 1934. The specific names, *rubeus* and *magnus* were incorrectly emended to *rubea* and *magna* respectively, apparently on the mistaken belief that *Stomachicola* is a feminine name. Yamaguti (1971) listed the species as *S. rubeus* and *S. magnus*.

Sinclair *et al.* (1972) suppressed *S. magna* (Manter, 1931) Manter, 1947 as a synonym of *S. rubea* (Linton, 1910) Manter, 1947. Furthermore, they predicated, (page 253) "an additional synonymy with *S. rubea* is the designation *Distomum tornatum* (in part) of Linton (1901, 1905, 1940), later referred to as *Dinurus pinguis* by Linton (1940) and Dawes (1940) and as *Tubulovesicula pinguis* by Manter (1947, 1954), Skrjabin and Guschanskaia (1954), Yamaguti (1958), Sogandares (1959) and Overstreet (1968)."

Although the life-history of the species is unknown, Sinclair *et al.* (1972) reported that *S. rubeus* uses a large number of small fishes as "transfer hosts." According to the report, these small fishes become infected in late spring or early summer; growth of the worms is continuous; and they wander freely in the body cavity or tissues, often invading the liver, spleen, heart, kidney, swim bladder and somatic musculature. Such worms are able to attain full maturity, often leaving trails of eggs in tissues during passage. Response by their hosts eventually kills the worms which become enclosed in melanated cysts and "mummified" in late winter or early spring. Larger fishes become infected by eating "transfer hosts." The only fishes recognized as "true" definitive hosts were the eel, *Anguilla rostrata*; tarpon, *Megalops atlantica*; lizardfish, *Synodus foetens*; and the kingfish, *Menticirrhus americanus*. In these fishes, the worms, acquired by ingestion of transfer hosts, remain in the stomach. Accordingly, the authors regarded *T. pinguis* as merely a young form of *S. rubeus*. They noted that *M. americanus*, when small, was one of the more common transfer hosts, but carried *S. rubeus* in the stomach when it reached a larger size (about 30 cm). This dual site of infection in the same host species, depending on the size of the host, suggested that residence in a transfer host is a necessary part of the life-cycle of *S. rubeus*, since it is unlikely that the definitive hosts acquire the infection from the host (probably a small crustacean) that harbors the metacercaria. Tracing the growth of the parasite in *Synodus foetens*, they reported that in June, 32 worms had a total length of 0.96-4.96 mm (av. 2.52) with the ecsoma contributing 0-62 (av. 42%) of this length. By early September, 128 worms ranged in size from 1.28-9.55 mm (av. 5.99) with the ecsoma contributing 0-77 (av. 61%). By early October, 16 specimens had the following lengths: 3.0-9.7 (av. 8.24 mm); ecsoma 33-79 (av. 64%) of the total length. In *M. americanus* and *Cynoscion* spp., the worms attained a length of

9.44–14.40 mm by mid-winter and from the pattern of growth it would appear that the larger worms (22–25 mm) of this species could be more than one year of age. However there was no statement concerning the sites from which these specimens were taken, and since the same host species may serve as both transfer and definitive host, the data are of doubtful value.

Dinurus rubeus was described by Linton (1910) from *Lycodontis moringa* and *Lycodontis funebris* taken at Dry Tortugas, Florida. Specimens measured 22 mm in maximum length and 1.5 to 2.00 mm in greatest width. In a large specimen the oral sucker was 0.98, the acetabulum was 1.92, and the pharynx 0.42 mm in diameter. In Figure 151, of a total mount, the acetabulum is less than its diameter posterior to the oral sucker and the gonads are in the anterior one-fifth of the body length. *Dinurus magnus* Manter, 1931 was *Distoma tornatum* Linton, 1905 renamed. The specimens were from *Synodus foetus* and *Cynoscion nebulosus* taken at Beaufort, North Carolina. The sizes agreed with the measurements of *D. rubeus*, with the ecsoma about two-thirds of the total length. Manter (1931) distinguished *D. magnus* by a short pars prostatica and the extent of the seminal vesicle. As noted, Yamaguti (1934) erected the genera *Tubulovesicula* and *Stomachicola*. *Stomachicola* was based on *S. muraenescois*, the type species. The worms are very long and slender, with the ecsoma some ten times as long as the trunk. The type specimen (Yamaguti, 1934, figures 105, 106) is 40.8 mm long and 1.89 mm wide. The largest immature specimen was 10.2 mm long and the largest mature one was 55 mm long. *Tubulovesicula* and *Stomachicola* were included in the subfamily Dinurinae Looss, 1907 but Yamaguti (1958) named *Stomachicola* type of a new subfamily Stomachicolinae in the family Hemiuridae. Yamaguti (1934) distinguished between *Stomachicola* and *Tubulovesicula* on the shape of the body, relative length of the ecsoma, and details in the shape of the seminal vesicle and extent of the pars prostatica. Manter (1947) transferred *D. rubeus* and *D. magnus* to *Stomachicola*. In *Tubulovesicula* the body is fusiform and the ecsoma, although variable in length, ordinarily is not more than one-half the total length.

The enigma posed by Sinclair *et al.* (1972) results from lack of information concerning the species under consideration. Unfortunately, the life-cycles of marine hemiurid trematodes are virtually unknown and evaluation of morphological data is dependent on knowledge of comparable features in other groups. The argument by Sinclair *et al.* that *S. magnus* is identical with *S. rubeus* is plausible but it is difficult to accept the identity of *T. pinguis* and *S. rubeus*. The idea that fully mature and gravid specimens of *T. pinguis*, four mm in length, if ingested by a larger host, can grow to a length of 20 mm or more and become stomachicolid in form, is contrary to accepted tenets of trematode development. It seems more probable that two closely related species may live simultaneously in the same host and that distinguishing features are not readily apparent. It is true that *T. pinguis* is primarily a parasite of the coelom and tissues but the worms must penetrate the wall of the digestive tract to enter the body cavity, and since only a few are present at any one time, they may be able to return. One distressing problem is to explain the fate of eggs shed by the worms in the closed coelom of *M. menidia*. If *T. pinguis* is merely a developmental stage of *S. rubeus*, the integrity of the genera is disrupted and the status of the several species assigned to the two genera becomes equivocal.

Systematic considerations

The trematodes from the stomachs of fishes constitute a large and diverse collection of genera, assigned by different authors to some twenty families in the superfamily Hemiuroidea Faust, 1929, the equivalent of the suborder Hemiurata Skrjabin and Gushanskaya, 1954. They have been known since ancient times and the name of the giant trematode from scombriform fishes, *Hirudinella marina* Garcin, 1730, is pre-Linnean. These worms are unique; they differ from other trematodes in structure and especially in the larval and developmental stages. In general, the body is strongly muscular, only slightly flattened, although in different groups, different regions of the body may be modified as adaptive responses to locations in their hosts and to subjective pressures. In certain species, the oral sucker may be retracted within the body and in one group, which includes *Tubulovesicula* and *Stomachicola*, designated as appendiculate, the posterior portion of the body may be retracted within the anterior portion. Looss (1907) discussed the morphology of these flukes and pointed out that the retractile region is not a tail. He designated the anterior region as the soma and the retractile region as the abdomen. It was described as the ecsoma (appendix) by Nicoll (1915). Looss described the effect of contraction on the topography of the organs. The first comprehensive treatise on the systematics of the group was predicted by Odhner (1911) in the statement, page 528, "Mit der Erkenntnis dass alle Magen-distomen bei Fischen in verwandtschaftlichen Beziehungen auseinander stehen, sind wir wieder um ein gutes Stück nach vorwärts gegen das natürliche Digenensystem gekommen, und die eigentümlichen Hemiuriden haben durch ihre Ableitung von den Azygiiden einen morphologischen Hintergrund bekommen. Früher (1907) habe ich schon die Didymozoiden von den Hemiuriden abgeleitet, eine Auffassung die sich seither bei mir nur erhärtet hat, und ich fühle also in natürlichem System der Digenea die familien Azygiidae Odhn., Hemiuridae Lühe, und Didymozoidae Montic. in dieser Ordnung nacheinander auf."

The same taxonomic concept was espoused by Fuhrmann (1928). He observed, page 98, "Näher oder entfernter verwandt sind alle *Magen-Distomeen* der Fische, die eine grosse Entwicklungsreihe zu bilden scheinen, welche mit den Azygiidae beginnt und in der formenreichen (30 Genera), reich verzweigten Gruppe der Hemiuridae gipfelt." He noted that certain members of the group have migrated from the stomach, some to the intestine, some to the gall-bladder, some to the swim-bladder, while others have moved forward into the mouth and gills. From these considerations he concluded, "Aus solchen Formen sind dann wohl die eigentümlichen Zystenparasiten der Familie der Didymozoonidae hervorgegangen."

With increase in number of described species and genera, the families listed by Odhner have been elevated to higher taxonomic categories. They have been dismembered and new taxonomic units have been proposed. The classification of these trematodes has sustained numerous revisions and no system is universally accepted. The worms are chiefly parasitic in marine fishes but are encountered, though much more rarely, in migratory and freshwater fishes, and members of the family Halipegidae Poche, 1925 occur in amphibians. They have been reported from lizards and snakes but it is possible that these records are concerned with predation. The earlier arrangements were based almost entirely on the morphology of adult worms, since data on life-cycles and larvae are meager and relatively recent.

Dollfus (1923) erected a superfamily Hemiurida, to contain the Hemiuridae Lühle, 1901, Accacoeliidae Looss, 1912, and Syncoeliidae Dollfus, 1923. Poche (1926) recognized the superfamily, in which he included five families: Hemiuridae Lühle, 1901; Azygiidae Odhner, 1911, and three new families Halipegidae, Isoparorchiiidae, and Xenoperidae. Faust (1929) included the same families in a superfamily which he named Hemiuroidea. Markevich (1951) proposed the order, Hemiurata, but did not list the constituent families. Skrjabin and Gushanskaya (1954) demoted the Hemiurata to the rank of a suborder with a single superfamily, Hemiuroidea Faust. They accepted the five families of Poche and in the suborder included the following families: Accacoeliidae Looss, 1912; Hirudinellidae Dollfus, 1932; Syncoeliidae Dollfus, 1923; Haplospalchnidae Poche, 1925; Coitocaccidae Ozaki, 1929; Bathycotyliidae Dollfus, 1932; Sclerodistomatidae Dollfus, 1932, Ptychogonimidae Dollfus, 1936; and Derogenetidae Dollfus, 1950. In a revision, Skrjabin and Gushanskaya (1956) divided the Hemiurata into two superfamilies: the Hemiuroidea Faust, 1929 in which the hermaphroditic duct is free in the parenchyma, and the Azygioidea which have a true genital bursa. The latter superfamily contained the families Azygiidae Odhner, 1911; Hirudinellidae Dollfus, 1932; Xenoperidae Poche, 1925; and Liocercidae Skrjabin and Gushanskaya, 1956. In a further revision, Skrjabin and Gushanskaya (1960), the Hemiuroidea was reconstituted with fifteen families, including six new ones: Dinuridae Skrjabin and Gushanskaya, 1954; Lecithasteridae Skrjabin and Gushanskaya, 1954; Lampri-trematidae Skrjabin and Gushanskaya, 1954; Elytrophallidae Skrjabin and Gushanskaya, 1954; and Aerobiotrematidae Yamaguti, 1958. Skrjabin and Gushanskaya (1960) did not recognize the Didymozoidae Poche, 1907 (Didymozoonidae Monticelli, 1888, renamed) as members of the Hemiurata.

LaRue (1957) proposed a new system of classification based primarily on life-history data and particularly on the development of the excretory bladder and associated structures. Two distinct superorders were recognized: The Anepitheliocystidia, in which the bladder remains membranous, and the Epitheliocystidia, in which the bladder is enclosed in mesodermal cells and its wall becomes epithelial. In his system, LaRue accepted the superfamily Azygoidea Skrjabin and Gushanskaya, 1956, which was elevated to the Azygiata, one of four suborders in the order Strigeatoidea (Anepitheliocystidia). The Azygiata contained two superfamilies: Azygioidea with two families, Azygiidae Odhner, 1911 and Bivesiculidae Yamaguti, 1939, and a new superfamily Transversotrematoidea with the lone family Transversotrematidae, Yamaguti, 1953. The Hemiurata Skrjabin and Gushanskaya, 1954 was included as one of two suborders in the order Opisthorchiida (Epitheliocystidia). It contained nine families: Hemiuridae, Halipegidae, Dinuridae, Lecithasteridae, Lecithochiridae, Bathycotyliidae, Isoparochiidae, Ptychogonimidae, and Didymozoidae. The relegation of the families Azygiidae and Didymozoidae to different superorders was a striking departure from previous arrangements. Moreover, recent electron microscope studies by Krupa, Cousineau and Bal (1969) have confirmed the observations of Stunkard (1930), that the wall of the excretory bladder in *Cryptocotyle lingua* is syncytial and similar findings were reported for other species by Powell (1972).

Adopting a proposal advanced by Marie Lebour (1912) and supported in part by Sewell (1922), Dubois (1929) and Dollfus (1949), Odening (1960) erected a new system of classification. The Digenea were divided into two subclasses,

Sporocystoidei and Redioidei, based on the type of larva produced in the primary host. In the former category, the cercariae develop in sporocysts; in the latter, they develop in rediae. In the scheme of Odening, the Hemiurata, Didymozoata Skrjabin and Sul'c, 1933, and Azygiata were included in the Redioidei.

Baer and Joyeux (1961) divided the class Trematoda into three subclasses: Aspidogastrea, Digenea, and a new subclass, Didymozoidea. In their treatment of the Digenea, they adopted the arrangement of LaRue (1957) for the Azygiata and the Hemiurata: twenty three families were included in the superfamily Hemiuroidea. The subclass Didymozoidea contained only the family Didymozoonidae Monticelli, 1888, with twenty-two genera. The removal of the Didymozoidae from the Digenea was based on their peculiar and aberrant morphology, on the development of gonochorism, and on a postulated direct development resulting from observations of Ishii (1935) and of Grabda (1947). The arrangement by Baer and Joyeux was analyzed and rejected by Stunkard (1963).

In a monograph on the trematodes of Brazil, Travassos, de Freitas, and Kohn (1969) revised the classification of the Digenea, changed the names of the orders by the use of a new ending, -formes, and described the species reported from Brazil. The Digenea contained thirteen orders and eighty-nine families. In the Hemiuriformes, they included nine families: Didymozoidae, Hemiuridae, Lecithochiriidae, Elytrophallidae, Isoparorchidae, Dinuridae, and Mabiaramidae Freitas and Kohn, 1967. In the Didymozoidae, they listed only one species, *Unitubulotestis sardae* (MacCallum and MacCallum, 1916) Yamaguti, 1952 from the gills of *Sarda sarda*. The family Mabiaramidae contained a single species, *Mabiarama provesiculata* Freitas and Kohn, 1967, from the stomach of *Rachycentron canadus*.

The most recent contribution to systematics of the hemiurid trematodes, is in the monumental, *Synopsis of Digenetic Trematodes of Vertebrates*, by Yamaguti (1971). This is a revision and amplification of his volume I (1958) in the series, *Systema Helminthum*. As formerly, the parasites are arranged under primary divisions based on their hosts, but new information when available has been employed in the disposition of families. The classifications of the Digenea above the family level proposed by LaRue (1957), Odening (1960), and Travassos *et al.* (1969) were not accepted. Because information on life-histories of these flukes is so fragmentary, and for many groups entirely absent, Yamaguti accepted only a few superfamilies and in the majority of instances, no attempt was made to refer families to higher taxonomic categories. The Azygiidae, for example, are unplaced although three subfamilies are recognized. The superfamily Hemiuroidea is restricted to eight families: Hemiuridae, Mabiaramidae, Ptychogonimidae, Prosogonotrematidae, Bathycotyliidae, Hirudinellidae, Lampritrematidae, and Sclerodistomidae. The Hemiuridae contains twenty-five subfamilies, many of them demoted from family status of other authors. The superfamily Didymozoidea (Monticelli, 1888) emend., is accepted with the single family Didymozoidae and twenty-four subfamilies. A new superfamily, Isoparochioidea was erected to contain seven families, whose species occur in the swimbladder rather than the stomach of fishes. The Accacoeliidae were removed from the Hemiuroidea, since their cercariae are not cystophorous, and assigned to a superfamily, Accacoelioidea, as suggested by Dollfus (1960a).

In the course of the past hundred years, a large number of trematodes have been described, many on inadequate and erroneous information and based often on

a single specimen. New genera and higher taxonomic categories have been erected to receive these dubious species. Among the hemiurid species, lack of information on life-cycles and larval stages has limited descriptions to features of sexually mature specimens. Consequently, specific and generic diagnoses are often indefinite and uncertain. Indeed, Nasir and Diaz (1971) have suppressed *Synaptobothrium* v. Linstow, 1904; *Plerurus* Looss, 1907; *Sterrhurus* Looss, 1907; *Separogermiductus* Skrjabin and Gushauskaya, 1955; and *Magniscyphus* Reid, Coil and Kuntz, 1965 as synonyms of *Lecithochirium* Lühe, 1901.

Discussing phylogeny of the divers groups of Trematodes, Baer and Joyeux (1961), observed, page 657, "On a décrit jusqu' à aujourd' hui plus de mille genres de Trématodes groupés en quelque cent familles don plusieurs monotypiques. On peut cependant affiner que cette pléthore de genres ne correspond nullement à la réalité et que leur nombre sera certainement réduit dans une proportion notable lorsque les auteurs entreprendront une revision sérieuse. On constate trop souvent que des caractères spécifiques sont prétextes à créer des genres nouveaux, sans même que la limite morphologique de ceux-ci ait fait l'objet d'une investigation sérieuse. L'emploi abusif de clés dichotomiques trop simples, c'est à dire qui sont fondées principalement sur des caractères superficiels ou variables, conduit, inévitablement vers une situation inextricable dont la conséquence est de surcharger la littérature scientifique d'une nomenclature aussi encombrante qu'inutile. L'existence de près de trente familles monotypiques accentue le malaise taxonomique que l'on ressent en face due système actual dont le nombre des sous-familles monotypiques est également trop élevé, laissant l'impression que le choix des bases de la classification des trématodes est arbitraire."

The genetic and taxonomic relations of the hemiuroid trematodes are yet obscure. They comprise a homogeneous, monophyletic group of digenetic forms. Primarily parasitic in the stomachs of marine fishes, some of them have migrated to other organs, some have invaded freshwater hosts, and members of one family, the Halipegidae, infect amphibians. Classification is based almost entirely on the adult generation since knowledge of life-cycles and developmental stages is meager. Life-cycles have been elucidated for several halipegid species, but this is a peripheral area in which events are probably greatly modified. For marine species a few life-cycles have been pieced together, but only one, that of *Lecithaster confusus* Odhner, 1905, has been experimentally demonstrated (Humminen and Cable, 1943). As their hosts evolved and occupied new environments, there have been corresponding changes in the morphology, physiology and development of their parasites. Differences of opinion on the significance of particular features have led to the formation of diverse taxonomic arrangements as noted above. Minor variations have been overemphasized with the unjustified multiplication of taxonomic units, as observed by Baer and Joyeux (1961). When adequate information on life-cycles and developmental stages becomes available, existing differences may be explicable, differences of opinion may be resolved, and an acceptable system of classification may be formulated.

Life-cycles and classification

The wide divergence of opinion concerning the systematics and classification of the hemiurid trematodes is the result, in large measure, of lack of knowledge of

their life-cycles and developmental stages. Data are meager, fragmentary, often faulty, and sometimes erroneous. Observations extend back for more than a century, (*q.v.* Dollfus, 1923, 1950a, 1954, 1960b) and unencysted metacercariae have been found in tow-nettings, and in a variety of planktonic organisms, chiefly crustaceans, ctenophores and chaetognaths. Dollfus (1923) noted that it is difficult if not impossible to recognize the adult stages and identify the larvae. He listed references to twenty-four species that occur in marine invertebrates. In addition, he noted that encysted progenetic metacercariae had been reported from various teleost fishes. Since the worms were gravid, they had been identified and referred to *Lecithochirium rufoviride* (Rudolphi, 1819) Lühe, 1901, to *Lecithochirium gravidum* Looss, 1907, and to *Synaptobothrium caudiporum* (Rudolphi, 1819) v. Linstow, 1904. The three species were included in the subfamily Sterrhurinae. Dollfus (1950a) enumerated the five essential characters of the cystophorous cercariae and listed the hosts and geographic distribution of the designated species. Thirty-nine species were described from gastropod hosts and one, *Cercaria prenanti* Arvy, 1940, from the scaphopod, *Dentalium dalli* taken off the northwest coast of France. This species was reported by Ching (1960) from the Pacific coast of the United States, at Friday Harbor, Washington. Contrary to earlier statements, Dollfus (1950a) predicated that all cystophorous cercariae belong in the superfamily Hemiuroidea; that the group is homogeneous and contains only those species in which the cercariae are cystophorous.

In a supplemental report, Dollfus (1960b) published a list of the distomes of chaetognaths, including those assigned to the Hemiuroidea. He predicated that the chaetognaths ingest the worms with food, either directly or in copepods or other small planktonic invertebrates which harbor the larvae. Thus, they may be either secondary intermediate hosts or merely facultative and supplementary associates intercalated in the life-cycle.

Szidat, Angelescu and Siccardi (1950) identified mature worms from the abdominal cavity of *Clupea melanostoma* taken in the Rio de la Plata, Argentina, as *Dinurus breviductus* Looss, 1907. Some were alive, others dead, and the disintegrated remains of others were centers of melanistic capsules containing eggs. Other small immature specimens were in caseous nodules on the wall of the stomach of *Raphiodon* (= *Cynodon*) *vulpinus* from the same locality. The normal host of *Dinurus breviductus* is *Coryphaena* sp., and Szidat *et al.* (1950) considered *Clupea melanostoma*, a freshwater species, to be an ancillary intermediate host, a "segundo huesped auxilliar." Commenting on this report, Dollfus (1954) declared that the worms encysted in teleost fishes, that earlier he had regarded as progenetic metacercariae, were actually adults which had perished in an aberrant host and outside their normal habitat in the intestine. He observed that the "cysts" were not secreted by the parasite but were connective tissue capsules produced by the hosts as a reaction to invasion. He cited other examples of hemiurid worms that had become mature in abnormal situations. The account by Sinclair *et al.* (1972) recalls the earlier one by Szidat *et al.* and in both instances the parasites had been assigned to the genus *Dinurus*.

The position of the Didymozoidae is equivocal. They are tissue parasites of marine and rarely, of freshwater fishes. They occur in the mouth, gills, skin, body cavity, muscles and connective tissue. In part they are cyst-dwelling, often in

pairs, with partial or complete separation of sexes. Some are monostomes, others are distomes, and the peculiarities of morphology are clearly adaptations to the tensions imposed by their locations in their hosts. Ishii (1935) reported direct development of *Didymocystis katsurconicola*. The embryonated eggs measured 0.017 to 0.019 mm in length and 0.010 to 0.012 mm in width. Each contained a larva whose anterior end bore a sucker and a double crown of alternating large and small spines. The penetration of the larva into the branchial epithelium was not observed, but similar larvae, about 1.0 mm in length, were found under the epithelium and it was presumed that the miracidium had transformed into the juvenile. Grabda (1947) made similar observations on the life-cycle of *Nematobothrium sardae* at the Varna Laboratory on the Black Sea. He found the worms in pairs on the gills of fishes, and reported penetration of young worms into the tissue. However, he stated, page 175, "L'auteur est parvenu à examiner à quatre reprises, la pénétration des individus du parasite dans la branchie du poisson. Malheureusement ces observations n'ont été faites que la préparations fixées." The accounts of Ishii and Grabda present no evidence that the miracidium penetrates the epithelium of the gills of fishes and Yamaguti (1958) questioned the account of Ishii. Developmental stages that appear to be didymozoid cercariae have been discovered in marine snails and unencysted metacercariae in crustaceans and juveniles in the intestine of small fishes portend a digenetic life-cycle. The statement of Yamaguti (1971, page 334) apparently establishes a digenetic cycle, with developmental stages from those found in crustaceans to those developing in the final hosts.

Skrjabin and Gushanskaya (1954) observed that complete life-cycles of members of the Hemiurata, for the most part, are known only for species in freshwater hosts. They noted that this is not surprising since freshwater conditions facilitate experimentation. These freshwater species are members of the family Halipegidae. The group is unique since it occurs in both marine and freshwater fishes and in both caudate and anuran amphibian hosts. Life-cycles are known for members of three genera, *Halipegus*, *Azygia*, and *Protocrometra*. In the genus *Halipegus*, life-cycles are known for four species. The type, *H. ovocaudatus* (Vulpian, 1858) Looss, 1899 occurs in the oral cavity and esophagus of European frogs. Leuckart (1886) obtained experimental infections of *Planorbis planorbis* by feeding eggs of the parasite. In collaboration with a student, Creutzburg, Leuckart (1889) observed the emergence of the miracidium from the egg, the development of the generations in the snail and the formation of the cercaria, identified as *Cercaria cystophora* Wagener, 1886. The descriptions of the experiments and results were included in the dissertation of Creutzburg (1890). Sinitzin (1905) reported that *Cercaria cystophora* from *Planorbis marginatus* is eaten by nymphs of the dragonfly, *Calopteryx virgo*, develops in the hemocoel, and is the larva of *H. ovocaudatus*.

The life-cycles of American species have been worked out for *Halipegus occidialis* Stafford, 1905 by Krull (1935); for *Halipegus eccentricus* Thomas, 1937 by Thomas (1939); and for *Halipegus anherstensis* Rankin, 1944 by Rankin (1944). Thomas reported that the young worms remain in the stomach of tadpoles until metamorphosis, when they migrate to the oral cavity and Eustachian tubes. In all of these studies, the cystophorous cercariae were ingested by copepods and developed as unencysted metacercariae in the hemocoel of the crustaceans. Metacercariae were found as natural infections in both dragonflies and damselflies but experimental infections of nymphs were not obtained. Macy, Cook and DeMott

(1960) found that in Oregon, the cercariae of *H. occidualis* are ingested by ostracods, *Capridopsis vidua* (O. F. Müller), which serve as second intermediate hosts in that area. They proposed the term, Cercariocyst, for the cercaria of halipegoid species. They found natural infections in dragonflies but stated, (1960, page 15) "Clearly, dragonfly nymphs are unnecessary for the completion of the cycle and become infected simply because they happen to eat ostracods along with other food." Adult worms were recovered from *Taricha granulosa* that had been fed infected ostracods.

Knowledge of azygiid life-cycles date from the report of Szidat (1932) that *Cercaria mirabilis* Braun, 1891, from *Lymnaca palustris* develops in *Esox lucius* and is the larva of *Azygia lucii* (Müller, 1776) Lühe, 1909, a common parasite in the stomach of salmonid fishes, especially species of *Esox*, in Europe. Life-cycles of North American species have been worked out for *Azygia sebago* Ward, 1910 by Stunkard (1956); for *A. acuminata* Goldberger, 1911 by Wootton (1957); and for *A. longa* Leidy, 1851 by Sillman (1962).

Members of the azygiid genus *Proterometra* Horsfall, 1933 also occur in North American freshwater fishes. Life-cycles have been elucidated for seven species: *Proterometra macrostoma* (Faust, 1919) Horsfall, 1933 by Horsfall (1934) and by Dickerman (1934); *Proterometra catenaria* Smith, 1934 by Smith (1934); *Proterometra hogesiana* Smith, 1936, by Smith (1936); *P. sagittaria* Dickerman, 1946 by Dickerman (1946); *Proterometra dickermani* Anderson, 1962 by Anderson and Anderson (1963); *Proterometra albicauda* and *Proterometra septimac*, both described by Anderson and Anderson (1967) with life-cycles recorded in the same publication. Anderson and Anderson (1963) reported that *P. dickermani* from *Goniobasis livescens* completes the life-cycle in the snail host. Metacercariae become gravid in the mollusk; eggs were embryonated and miracidia were obtained. They may produce new infections in the same snail or, if eggs are ingested, other snails may become infected. No naturally infected fishes were found but experimental infections were produced in sunfishes, *Lepomis* spp. and bass, *Micropteroideus salmoides*.

Stages in the life-history of other halipegoid species are known at least in part. Dollfus (1950b) described *Halipegus africanus* n. sp. from *Rana mascariensis* taken in the Belgian Congo and mature cystophorous cercariae in rediae from *Biomphalaria katongae*. The life-cycle was based on morphological agreement, not on experimental infection. Tang (1951) described *Genarchopsis chinensis* n.sp., from freshwater fishes in China with an account of the life-cycle. The cystophorous cercariae developed in *Melania foretiana*. The species was named type of a new genus, *Tangioopsis*, by Skrjabin and Gushanskaya (1955). Yamaguti (1954) reported cystophorous cercariae from *Semisulcospira libertina* which, when fed to *Cyclops* spp., developed into metacercariae with the characteristic features of the genus *Genarchopsis* Osaki, 1925 (syn. *Progonus* Looss, 1899; *Genarches* Looss, 1902, both names preoccupied). The genus has species in marine and freshwater fishes in Japan, Russia and India.

Genarchella genarchella Travassos, Artigas and Pereira, 1928 was described from the esophagus and stomach of *Acestrorhamphus* sp. in Brazil. Szidat (1956) found the larval generations in *Littoridina australis*. According to his account, the cercariae do not leave the rediae but become sexually mature and produce eggs. When infected snails are eaten, the eggs are liberated and the metacercariae grow

and again become gravid. He predicated that the old snails perish in late fall and winter and the rediae they contain, together with the gravid metacercariae, emerge into the water. Young specimens of *L. australis* become infected by eating the eggs with food. The miracidia emerge, develop into sporocysts in the liver and begin the formation of rediae.

A remarkable and anomalous situation obtains in the related genus *Bunocotyle* Odhner, 1928, which contains unusual parasites of freshwater fishes. The type species, *B. cingulata* Odhner, 1928 was described from *Perca fluviatilis* taken on the east coast of Greenland, from *Acerina cernus* of the Baltic, and from *Silurus glanis* of the Volga delta. The genus was designated type of the subfamily, Bunocotylineae Dollfus, 1950, which was included in the family Halipegidae by Skrjabin and Gushanskaya (1954) and in the family Hemiuridae by Yamaguti (1971). Chabaud and Biguet (1955) described cystophorous cercariae from *Hydrobia stagnalis* taken from a canal near the Étang-du-Canet (Pyrénées Orientales) and their development in copepods, *Poppella guernei*, to progenetic metacercariae that were identified as *Bunocotyle cingulata* Odhner, 1928. Markowski (1936) had described progenetic metacercariae from *Hydrobia ventricosa*, taken in the Baltic, as *Metorchis progenetica*. As many as fifty gravid worms were found in a single snail. Chabaud and Buttner (1959) showed that the larva described by Markowski (1936) is a species of *Bunocotyle* for which they proposed the name *Bunocotyle progenetica* (Markowski, 1936). They found heavy infections (environ 80%) of *H. stagnalis* at Canet, but were unable to find infected fishes in the area. The species, assigned to *B. cingulata* by Chabaud and Biguet (1955) was recognized on biological grounds as a new species, *Bunocotyle meridionalis*. They observed that life-cycles in the hemiurid trematodes may be extraordinarily varied, with one, two, three or four hosts. In the genus *Bunocotyle*, *B. progenetica* becomes mature in the mollusk; *B. meridionalis* becomes mature in the second intermediate host, the copepod; while *B. cingulata* matures in the piscine host. There is the possibility of a four-host-cycle when the copepod host is eaten by small fishes that serve as transport or paratenic hosts. Rebecq (1964) found *B. meridionalis* in *Hydrobia ventrosa* and *Hydrobia acuta* taken in the Camargue, a part of the Rhone delta near Marseille. The gravid metacercariae were found in *Calanipeda aquae-dulcis* (= *Popella guernei*).

The postulate by Sinclair *et al.* (1972) recalls the report by Dollfus (1950b) in which he noted that Looss, Nicoll, Szidat, and other authors had observed young sterrhurine worms encysted in the peritoneum and other organs of various teleost fishes. The significance of these findings is yet obscure and the tendency for larval stages of hemiurid trematodes to become sexually mature, renders interpretation of life-cycles very tenuous. The cystophorous cercariae are regularly eaten by copepods, and these in turn by small fishes where they may become mature in the stomach. Whether or not the mature worms, encysted in small fishes, constitute a stage in a normal life-cycle is questionable. It appears more likely that they are stray individuals in abnormal hosts, which have abandoned the stomach and are destined to perish and become encapsulated in connective tissue.

In the hemiurid trematodes the eggs are small, very numerous, embryonated when passed, and the miracidia emerge only after ingestion by a suitable molluscan host. These features suggest a high larval mortality and great hazards in the completion of the life-cycle. The miracidia of the hemiurid, azygiid and didymozoid species are unique and very similar. All are aciliate, provided with an anterior

circle of spines, and the surface of the body bears bristles, often disposed in radial plates at the anterior and sometimes also at the posterior end of the larva. The cercariae develop in rediae; they lack penetration and cystogenous glands and develop into the cystophorous stage which is characteristic for hemiurid trematodes. Typically they are eaten by copepods and the metacercariae occur as unencysted larvae in the hemocoel of the crustacean or other planktonic invertebrates that feed on copepods. Sexually mature worms occur in the stomach or in the body cavities of fishes or they may be encysted in the tissues, often in a dead or disintegrating condition. The striking similarity of the larval stages, and the fact that they are peculiar to the hemiurid trematodes, portends genetic homogeneity and despite adult adaptations to different situations, the thesis of Odhner and Fuhrmann that the Azygiidae, Hemiuridae and Didymozoidae are closely related is probably correct.

SUMMARY

Dinurus pinguis Linton, 1940 was described from a large collection of small trematodes, assembled during the previous forty years. Many of them had been assigned to other, different, species in earlier publications. There was no type-specimen but the account was based primarily on material from *Menidia menidia*. The specific diagnosis was indefinite, imprecise, and so general that it might include members of more than one genus. *Dinurus pinguis* was transferred by Manter (1947) to the genus *Tubulovesicula* Yamaguti, 1934. The species, as restricted, is common in *Menidia menida* at Woods Hole, Massachusetts and is redescribed from juvenile and adult specimens.

Sinclair, Smith and Sullivan (1972) suppressed *Stomachicola magnus* (Manter, 1931) Manter, 1947 as a synonym of *Stomachicola rubeus* (Linton, 1910) Manter, 1947 and predicated that *Tubulovesicula pinguis* is merely a stage in the life-cycle of *S. rubeus*. The identity of *S. rubeus* and *S. magnus* may be accepted, but the proposal that *T. pinguis* may develop into *S. rubeus* is rejected.

The collection, organization and integration of information on the genetic relations and systematics of the hemiurid trematodes discloses different interpretations and evaluations of taxonomic features. The present status is reviewed. The divergence of opinion results in large measure from lack of knowledge of life-cycles and developmental stages of marine species. Information from freshwater species, although limited, is significant and helpful. Homologous features, common to all hemiurid species, include the nature of the eggs, the peculiar bristle-bearing miracidia, the presence of rediae in the life-cycle, the characteristic cystophorous cercariae that are eaten by small crustaceans, and the unencysted metacercariae in various planktonic invertebrates. These striking features, shared by all members, portray a common genetic constitution and support the postulate of Odhner (1905), Fuhrmann (1928) and others that the Azygiidae, Hemiuridae and Didymozoidae are members of a common superfamily.

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